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Limnology of Lakes in Gates of the Arctic National Park and Preserve, Alaska

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ABSTRACT

LaPerriere, J. D., J. R. Jones and D. K. Swanson. 2003. Limnology of lakes in Gates of the Arctic National Park and Preserve, Alaska. Lake and Reserv. Manage. 19(2):108-121.

Limnological reconnaissance data were collected during summers 1992-93 and 1995 from 16 major lakes within Gates of the Arctic National Park and Preserve, Alaska (GAAR) located above the Arctic Circle. In GAAR the southern lakes (~67°N) and those in the Brooks Range foothills are in watersheds with taiga and tundra vegetation. The northern lakes (~68°N) are at higher elevations in the Brooks Range in watersheds that lie wholly beyond the treeline. Average sum of the cations for all lakes matches the world average for fresh waters and the average for drainage from tundra and taiga landscapes. Local lithography explains the measured decrease in calcium equivalents and silica, and an increase in magnesium with altitude because of more calcareous rock in the southern basins at low altitude and shale/conglomerate in northern mountain catchments. In most low altitude lakes Secchi depth was located in sub-surface algal peaks at temperatures averaging ~8.5 C cooler than the surface, typically with double the surface chlorophyll value. Mineral turbidity, and less so color, controlled transparency in several high altitude lakes where turbid inflows were a factor. Lakes were oligotrophic based on nutrients and algal chlorophyll, but a doubling of TP and concurrent halving of TN was measured in GAAR lakes with altitude. Both patterns were correlated with the decreasing density of terrestrial vegetation with altitude, resulting in a sharp decline in the TN:TP ratio. This pattern suggests sources of these nutrients change across the landscape continuum within GAAR described by altitude and vegetation zones. Nitrogen fixation associated with terrestrial vegetation most likely accounts for greater TN in lakes within the taiga and moist or wet tundra, whereas TN levels approximated the N content of regional rainfall in high elevation lakes with predominately barren land and prostrate shrub in the catchments. Ratios of TN:TP and Nutrient Stimulation Bioassays suggest P limitation was likely among low altitude lakes and N limitation increased in importance in lakes at high altitude. The particulate composition ratio (as C:N:P molar ratio) of these lakes averaged ~200:20:1.

Key Words: arctic lake, mountain lake, nitrogen, phosphorus, phytoplankton, water clarity.

Gates of the Arctic National Park and Preserve, Alaska (GAAR), located above the Arctic Circle, is the second largest national park in the nation; at 3.4 million hectares, it is about 10 times larger than Rhode Island (Fig. 1). It contains major portions of the Brooks Range and Endicott Mountains, and six national wild rivers originate within, or transect, the park. Despite its size and protected status, more is known about water resources beyond the park perimeter than within. Streams of the north slope of the Brooks Range have been surveyed and classified (Craig and McCart 1975), and the upper Kuparuk River located north and east has been intensively studied (Peterson 1985, Peterson et al. 1992, Hershey et al. 1997), as have lakes within the

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drainage (Kling et al. 1992). The long-term studies of Toolik Lake, located northeast of the boundary in the northern foothills of the Brooks Range, have been well-summarized by O'Brien et al. (1997) and data from lakes and streams within this basin have illustrated spatial patterns in an arctic landscape (Kling et al. 2000, Levine and Whalen 2001). Arctic tundra lakes north of the Brooks Range have also been sampled by Gregory-Eaves et al. (2000) as part of a statewide survey. Lakes and ponds in the Noatak River Valley, mostly west of the park, have been characterized for phytoplankton, primary productivity and algal nutrient limitation (O'Brien et al. 1975). Four lakes within the park – Kipmik (O'Brien et al. 1975), Walker (Jones et al.1990), Itkillik (LaPerriere and Jones 1991, Kling et al.1992) and Selby (LaPerriere et al. 1998) – have been studied with an emphasis on water chemistry, periphyton and nutrient limitation of algal biomass.

This paper summarizes limnological data collected during summers 1992-93, and 1995 from 16 major lakes within GAAR (Fig. 1) to establish baseline information on water chemistry, lake trophic status and nutrient limitation of phytoplankton. We draw on data from earlier studies where appropriate (Jones et al. 1990, LaPerriere and Jones 1991, LaPerriere et al. 1998) and contrast the findings with other studies of high latitude lakes.

Methods

Lakes were accessed at the deepest spot by airplanes on floats during mid-July 1992 and 1993 and about a week earlier in 1995 (Fig. 1, LaPerriere 1999); most but not all lakes were sampled each summer. Lake Minakokosa is located beyond the park boundary but was sampled because of its hydrologic link to the park (Fig. 1). Secchi transparency was measured using a standard 20 cm disk. In 1993 and 1995 the penetration of photosynthetically active radiation (PAR) was measured using a Li-Cor 185B quantum radiometer photometer with an LI-193SA spherical quantum sensor. Data were taken at each meter of depth until values decreased to approximately 1% of the irradiance measured immediately under the water surface ($I_{1\%}$)

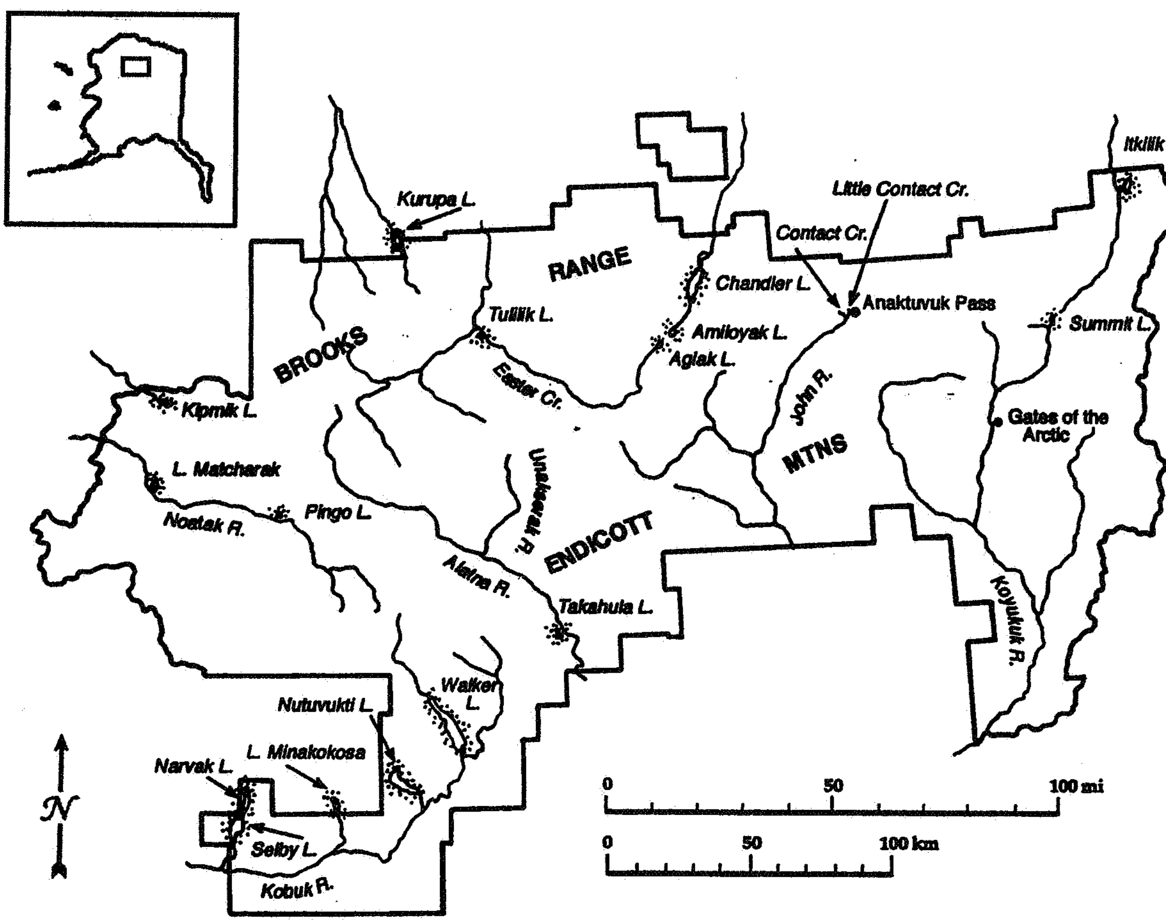

Figure 1.–Gates of the Arctic National Park and Preserve with study lakes and major streams.

and the vertical attenuation coefficient of downward irradiance, K_d, was calculated from these data.

In 1992, samples for water color and turbidity, major ions, and nutrients were taken in triplicate with an opaque 2 L Van Dorn sampler at a depth of 2 m, and delivered into 1 L cubitainers and placed in an insulated cooler. Trace metal samples were taken in the same way and delivered into new, acid pre-cleaned 250 mL Nalgene bottles and stored in a cooler. Also, in 1992 phytoplankton samples for algal chlorophyll were taken with the same sampler at depths of 1 m, the Secchi depth, and twice the Secchi depth. In 1993 and 1995, samplers were all integrated though depth with a weighted 13 mm (i.d.) Tygon tube lowered to twice the Secchi depth (Hanna and Peters 1991). Limited comparisons suggest that discrete and integrated samples provided comparable results.

Depth profiles of physical and chemical characteristics were taken using a YSI Model 3800 multi-meter fitted with depth, temperature, pH, conductivity, oxidation/reduction potential, and dissolved oxygen probes. Unit calibration was conducted every few days, and whenever any sensor maintenance was required. Readings of dissolved oxygen were corrected for altitude with a built-in barometer. Conductivity was automatically corrected to 25°C by the meter. Some measurements in 1993 were made with a YSI model 56 meter.

At a temporary laboratory in Bettles, AK apparent (unfiltered) color was read at 455 nm on a HACH Model 2000 spectrophotometer. Turbidity was read on a HACH Model 16800 Portalab turbidimeter in 1992-93 and in 1995 a HACH Model 2100P hand-held turbidimeter was used. All samples for planktonic chlorophyll were prepared by filtering 1 L samples through Gelman GF/C filters and were stored frozen over desiccant. Filters were extracted in hot ethanol and measured on a fluorometer (Satory and Grobbelaar 1984, Knowlton 1984). For phosphorus and nitrogen, triplicate samples were placed into acid-washed screw-cap culture tubes and N samples were preserved with 20 mL of 50% sulfuric acid. Persulfate digestion was carried out in all the tubes, and the molybdate blue species of P was read using a spectrophotometer. Nitrogen was read on nitrate formed during digestion by the second-derivative spectroscopy method of Crumpton et al. (1992). Organic carbon and nitrogen, filtered in 1993 at the field laboratory onto GF/C filters stored over desiccant, were measured at Iowa State University using a Carlo Erba CHN analyzer. Particulate phosphorus was estimated for these samples by taking the difference between total phosphorus and total dissolved phosphorus in the filtrate. This allowed us to estimate particulate composition ratios (Hecky et al.1993).

Alkalinity was titrated using the HACH digital titrator on 200 mL samples with 0.160 N sulfuric acid and bromcresol green-methyl red indicator. Chloride was titrated in 1992 and 1993 using the HACH digital titrator on 100 mL samples with 0.2256 N mercuric nitrate. Chloride was not measured in 1995 because previous collections showed concentrations were below the detection limit of 0.1 mg $\cdot L^{-1}$. Sulfate was measured using HACH's turbidimetric method using Accuvac Ampules (25 mL) read on the HACH Model 2000 spectrophotometer.

Trace metal samples were refrigerated at the field laboratory and shipped to Fairbanks where they were preserved with 0.3 mL of Ultrex-grade concentrated nitric acid, and then shipped to Environmental Trace Substance Research Laboratory, Columbia, MO, where they were acid digested for total recoverable metals and analyzed by induced coupled plasma spectroscopy scanning for 30 elements (LaPerriere 1999).

Nutrient stimulation bioassay experiments were conducted on Selby and Narvak lakes in 1993 (LaPerriere et al. 1998) and on Agiak, Chandler, Itkillik, Kipmik, Matcharak, and Summit lakes in 1995. Similar experiments were conducted at Walker Lake in 1988 (Jones et al. 1990) and at Itkillik Lake in 1989 (LaPerriere and Jones 1991). Near surface water was placed into 10 L cubitainers. Triplicate containers were treated with nitrogen (adding 75 $\mu g \cdot L^{-1}$ ammonium nitrate) with phosphorus (adding 5 $\mu g \cdot L^{-1}$ sodium orthophosphate), with both nutrients at these concentrations, and with no chemical amendments as controls. The cubitainers were attached to a line at one-half the Secchi depth and allowed to incubate at ambient conditions for 4 or 5 days. When retrieved, they were returned to the field laboratory in dark containers, and replicate subsamples were immediately filtered through GF/C filters and treated as all other chlorophyll samples. Treatments were compared using a Bonferroni test (alpha = 0.05).

Data from each lake were averaged to arrive at the lake mean used in our analyses. Lake means were normalized (log) when appropriate, and significance in correlation and regression analyses was set at 0.01 unless stated otherwise.

Geomorphology and Landscape Characteristics

Altitude and latitudinal location of each lake was read from topographic maps (Fig. 1, Table 1). Lake surface areas, volumes, and mean depths were measured on undated bathymetric maps by Reanier and Anderson

Table 1.–Geomorphic and morphometric characteristics of lakes of Gates of the Arctic National Park and Preserve (lakes are in order of increasing altitude).

	Altitude	Degrees Latitude	Longitude	Watershed Area	Surface Area	Volume	Mean Depth	Maximum Depth
	(m)	(N)	(W)	(km²)		(m³ x 10⁶)	(m)	
Minakokosa	137	66.93	155.02	94.0	3.2	114	35.5	54
Narvak	145	66.93	155.63	234.3	8.7	543	62.4	114
Selby	145	66.87	155.68	280.9	9.9	145	14.6	33
Nutuvukti	192	66.98	154.70	75.9	16.2	319	19.7	49
Walker	194	67.13	154.38	523.6	37.5	2297	61.4	122
Takahula	247	67.35	153.66	5.5	1.7	55	32.3	55
Matcharak	502	67.75	156.21	32.2	2.8	35	12.5	25
Pingo	540	67.67	155.41	6.1	0.7	–[a]	–	–
Tulilik	555	68.13	154.12	3.2	0.2	–	–	–
Itkillik	681	68.40	149.92	26.3	3.9	23	5.8	13
Kipmik	740	67.95	156.13	43.6	2.9	25	8.6	45
Chandler	888	68.22	152.71	341.2	12.8	181	14.1	22
Kurupa	925	68.34	154.64	173.5	4.6	67	14.6	37
Agiak	963	68.08	152.95	51.4	1.5	7.8	5.2	16
Amiloyak	970	68.11	152.86	26.9	1.1	4.1	3.9	10
Summit	1073	68.07	150.46	4.4	0.4	–	–	–

[a] Dash means bathymetric map not available.

(University of Washington) or on maps generated by GAAR personnel. Watershed areas were measured on 1:63,360 scale U.S. Geological Survey topographic maps. The land cover characteristics of each watershed were taken from a classification of Landsat Thematic Mapper satellite imagery (30 pixel resolution) by Earth Satellite Corporation (Rockville, MD, 1999). The classification includes 32 land cover classes, 25 of which occurred in the lake watersheds of this study. Land cover classification was not available for Itkillik Lake due to cloud shadow on the satellite image. The 25 land-cover classes were aggregated into six major groups for descriptive purposes in this paper; coverage for these six groups was estimated from 1:60,000 color-infrared aerial photographs in the Itkillik Lake watershed for which the satellite classification was lacking.

Results

Landscape and Geomorphology

In GAAR the southern lakes (~67°N) are at relatively low elevations in the foothills on the south side of the Brooks Range. These lakes are surrounded by forest but their watersheds extend beyond the treeline (Table 1, Fig. 1). The northern lakes (~68°N) are at higher elevations in the Brooks Range and lie wholly beyond the treeline. Thus, altitude and latitude are positively correlated ($r = 0.74$, $n = 16$). Several of the southern lakes lie in fjord-like troughs and are deeper than the northern lakes. The six lakes located on the south slope of the Brooks Range, at altitudes <250 m in the Kobuk and Alatna river drainages, are within the taiga zone with mostly spruce forest and tall shrub vegetation at low elevations and prostrate shrub vegetation or barren land above the treeline (Table 2). The five lakes at intermediate altitudes (>500 and <740 m, Matcharak, Pingo, Tulilik, Itkillik and Kipmik) have watersheds dominated by moist and wet tundra, and prostrate shrub with little tall shrub and some barrens. The northernmost five lakes, at elevations of 888 to1073 m, have more prostrate shrub and barrens, and less moist and wet tundra than the intermediate group (Table 2). Overall, watersheds of the study lakes show decreasing terrestrial vegetation biomass with increasing latitude and altitude. Quadratic equations show a significant increase in the proportion of barren land ($R^2 = 0.36$) and prostrate shrub ($R^2 = 0.72$) with altitude, while the proportion of tall shrub ($R^2 = 0.80$), white spruce/broadleaf forest ($R^2 = 0.73$) and black spruce/spruce woodland ($R^2 = 0.76$) decrease. The proportion of moist and wet tundra peaked at > 50% in lake basins at mid-altitudes ($R^2 = 0.61$, Table 2).

Ionic Salinity, Composition and Silica

Expressed as the sum of the cations, salinity in the GAAR lakes averaged 1.31 meq · L^{-1} (median = 0.845 meq · L^{-1}). Values ranged from 0.199 meq · L^{-1} in Agiak Lake, a headwater lake in the Brooks Range at 963 m, to 3.82 meq · L^{-1} in Pingo Lake, a shallow, oxbow/thermokarst lake located within the flood plain of the Noatak River (Fig. 1, Table 3). The overall average closely matches the world average for fresh waters (cation equivalents = 1.42 meq · L^{-1}, Wetzel 2001) and the average for drainage from tundra and taiga landscapes (cation equivalents = 1.38 meq · L^{-1}, Meybeck 1979). Among the GAAR lakes the relation between salinity and altitude was not linear because of patterns in the local lithography. Lakes with < 0.5 meq · L^{-1} cations (Agiak, Amiolak, Kipmik and Summit) were each located near the headwaters of their respective drainages (Fig. 1) where non-calcareous shale, sandstone and conglomerate occur. Cations varied between 0.58 and 0.85 meq · L^{-1} among low altitude lakes within the Kobuk River drainage (Minakokosa, Narvak, Nutuvukti and Selby) where a mixture of metamorphic, sedimentary, and volcanic rocks with minor amounts of carbonates occur. Lakes in watersheds with the greatest coverage by carbonate rocks (Walker, Itkillik and Takahula, in order of increasing proportion of carbonates) had cations of 1.35, 2.37 and 3.08 meq · L^{-1}, respectively. In all lakes pH measurements were alkaline, with no evidence of acidification.

The proportion of Ca and Mg equivalents were negatively correlated among the study lakes ($r = -0.96$, $n = 16$). Calcium accounted for >70% of cation equivalents in lakes with some calcareous rocks in the basin (Itkilik, Matcharak, Minakokosa, Narvak, Nutuvukti, Selby, Takahula and Walker). Eliminating oxbow Pingo Lake from the analysis, the proportion of Ca equivalents decreased with altitude ($r = -0.80$, $n = 15$) while there was an increase in proportion of Mg ($r = 0.74$) and Na ($r = 0.67$). This relation between cation composition and altitude reflects the greater presence of calcareous rock in the southern basins and shale (presumably with Mg-rich clay materials) in the north. Potassium accounted for <3% of the cation equivalents.

Anion equivalents were highly correlated to cations ($r = 0.99$, $n = 16$) but measurements of the negative ions averaged 10% less than cations (Table 3). The difference was negatively correlated with sulfate ($r = -0.72$, $n = 16$), suggesting the sensitivity of the analytical technique was a factor. Bicarbonate composed >80% of anion equivalents in most GAAR lakes but sulfate composed ~40% of the anions in those lakes where shale is important (Amiolak, Chandler and Kurupa) or where

Table 2.–Land cover in the catchments of lakes of Gates of the Arctic National Park and Preserve (data expressed as % of catchment and lakes are in order of increasing altitude).

	Altitude (m)	Barren	Prostrate Shrub	Moist and Wet Tundra	Tall Shrub	White Spruce or Broadleaf Forest	Black Spruce or Spruce Woodland
Minakokosa	137	3	8	13	21	15	40
Narvak	145	10	19	14	16	11	31
Selby	145	10	19	15	16	11	29
Nutuvukti	192	1	4	9	12	17	57
Walker	194	23	25	14	19	8	12
Takakula	247	19	18	7	4	23	29
Matcharak	502	5	41	48	6	0	0
Pingo	540	36	23	29	11	0	0
Tulilik	555	3	13	82	2	0	0
Itkillik	681	25	25	50	0	0	0
Kipmik	740	13	32	52	2	0	0
Chandler	888	32	33	34	1	0	0
Kurupa	925	42	40	18	0	0	0
Agiak	963	31	42	26	1	0	0
Amiolak	970	36	32	32	0	0	0
Summit	1073	14	61	25	1	0	0

Table 3.–Total cations and anions (as meq·L^{-1}); total phosphorus (TP), total nitrogen (TN), algal chlorophyll (Chl), particulate organic carbon (POC from 1993) and particulate organic nitrogen (PON from 1993) (as µg ·L^{-1}) and silica (as mg·L^{-1}) in lakes of Gates of the Arctic National Park and Preserve (lakes are in order of increasing altitude). Results of Nutrient Stimulation Bioassays (NSB) are listed as a significant response to phosphorus (P), nitrogen (N) or light (L) relative to a control.

	Cation	Anion	TP	TN	Chl	POC	PON	SiO_2	NSB
	meq·L^{-1}		µg·L^{-1}					mg·L^{-1}	
Minakokosa[c]	0.640	0.507	6	360	1.9	–[d]	–	2.1	–
Narvak[a]	0.849	0.928	4	360	1.4	106	13	1.7	P
Selby[c]	0.814	0.905	3	320	1.3	99	12	1.6	P
Nutuvukti[a]	0.585	0.478	5	250	1.6	153	19	0.7	P
Walker[b]	1.351	1.251	4	300	1.0	72	6	1.0	P
Takahula[b]	3.080	3.031	3	207	1.1	122	12	1.3	–
Matcharak[b]	2.440	2.443	8	360	2.3	330	39	1.7	N
Pingo[c]	3.817	3.119	15	765	2.1	–	–	0.7	–
Tulilik[c]	1.448	1.104	7	445	1.4	–	–	0.7	–
Itkillik[a]	2.365	2.149	6	260	1.3	183	25	0.8	N
Kipmik[b]	0.250	0.170	5	155	2.2	222	26	0.6	N
Chandler[b]	0.842	0.890	6	155	1.2	207	21	0.6	L
Kurupa[c]	1.532	1.530	11	125	0.5	–	–	1.0	–
Agiak[a]	0.199	0.133	8	130	1.7	239	31	0.5	N
Amiloyak[a]	0.384	0.471	9	175	1.7	279	37	0.8	–
Summit[a]	0.344	0.210	13	150	1.9	213	26	0.7	N

[a] Two years.
[b] Three years.
[c] One year.
[d] Dash means data were not collected.

volcanic rock occurs (Minakakosa, Selby and Narvak). Chloride composed <2% of the anions.

Silica varied between 0.5 and 2.1 mg·L^{-1} among the sampled lakes (Table 2) and was negatively correlated with altitude ($r = -0.65$, $n = 16$). The largest value was measured in Lake Minakokosa where volcanic rock occurs.

Thermal Characteristics and Oxygen

Several northerly lakes within GAAR (Amiloyak, Chandler, Itkillik and Kurupa) had bottom temperatures >5°C and did not permanently stratify during summer because of shallow depth and frequent, strong winds. Depending on depth and fetch, these lakes are either continuous or discontinuous cold polymictic (Lewis 1983). For example, on 8 July 1989, Itkillik Lake was weakly stratified but days later winds mixed the lake to the bottom (Fig. 2a and b). By contast, several other shallow lakes at intermediate and high elevations had bottom temperatures >5°C and surface temperatures of 10 to 15°C, suggesting they are dimictic (Kipmik, Matcharak and Summit). Deep lakes (>30 m, Minakokosa, Narvak, Nutuvukti, Selby, Takahula and Walker) at altitudes <250 m in the Kobuk and Alatna River drainages showed summer stratification and are clearly dimictic (Figs. 2c-d, 3 and 4).

Temperatures colder than 4°C were found deep in several southern lakes in 1992 and 1995 (Minakokosa, Narvak, Nutuvukti, Takahula and Walker). The cold hypolimnion may result from the discharge of cold groundwater, perhaps associated with permafrost, in the basins and in some cases from missed vernal overturns. The vernal overturn is occasionally missed because summer stratification begins and strengthens under the ice, and winds at ice-off are insufficient to overturn the lake (LaPerriere 1981).

Measurements in 1993 coincided with an unusual arctic heat wave that caused the 12 July air temperature to reach 34°C at Selby Lake. During lake surveys collected 16-21 July 1993, maximum surface temperatures were measured: 14.5°C at Agiak, 15.2°C at Amiloyak, 11°C at Chandler, 14°C at Itkillik, 16.3°C at Kipmik, 18°C at Matcharak and Narvak, 23.4°C at

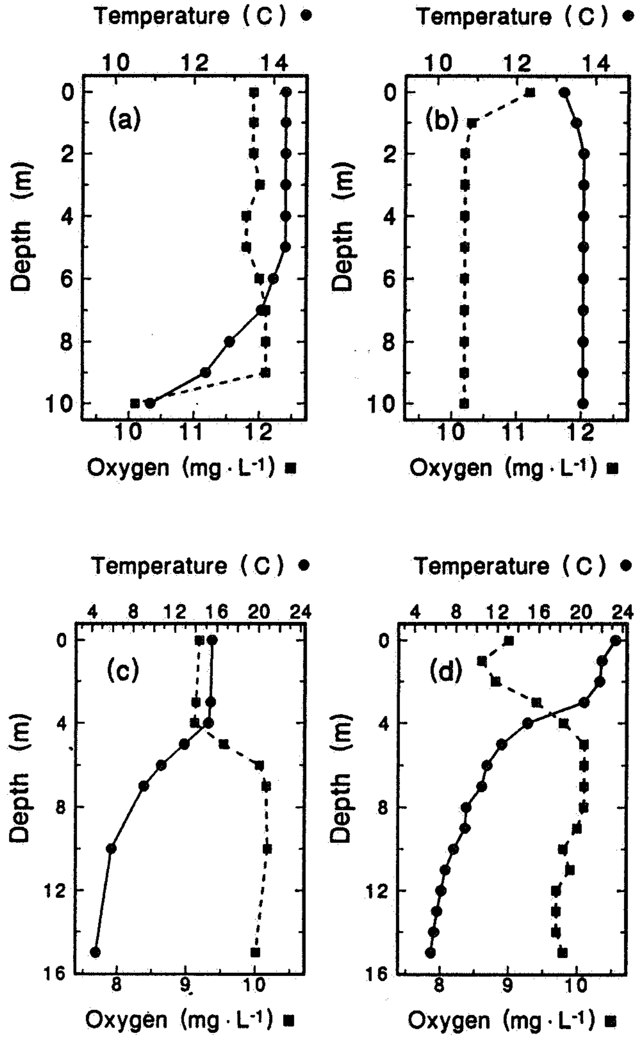

Figure 2.–Temperature and oxygen data collected from Itkillik Lake on 8 July 1989 (a), from Itkillik Lake on 12 July 1989 (b), from Nutuvukti Lake on 15 July 1992 (c), and from Nutuvukti Lake on 20 July 1993 (d).

Nutuvukti, 21.5°C at Selby, 14.2°C at Summit, 18.5°C at Takahula and 20°C at Walker. Therefore, Hobbie's (1973) rule that arctic lakes never warm above 15°C was violated, even by northerly lakes within GAAR (Kipmik and Matcharak). These peak surface temperatures in the GAAR lakes showed a strong decline with increasing altitude and latitude (r = >-0.84, n = 12). Near-bottom water temperatures in some of the polymictic lakes in 1993 were also highest in our collection: 10°C at Agiak, ~12°C at Amiloyak, 8°C at Chandler and ~14°C at Itkillik. In other years ~6°C was typical of Agiak and Chandler lakes.

Dissolved oxygen profiles in GAAR lakes were usually orthograde with >85% saturation at the lake bottom (Fig. 2). Subsurface oxygen peaks were also associated with thermoclines in several dimictic lakes (Fig. 3) and were probably due to algal photosynthesis within deep chlorophyll peaks that are a common feature of the deep, stratified lakes (Fig. 4, Jones et al. 1990, LaPerriere et al. 1998). Often subsurface chlorophyll values were double the surface concentration, and in some cases the increase was >5-fold (LaPerriere 1999). Greater oxygen depletion (<70% saturation at the bottom) was measured in some lake samples (Kipmik, Matcharak, Minakokosa, Nutuvukti and Takahula). Several of these lakes receive seepage water from organic-rich, waterlogged, and therefore anaerobic soils which also contributes to oxygen depletion, as does decomposition of autochthonous material. The phenomenon is described by Hobbie (1973) wherein cooling, sinking water from the shallows is deoxygenated by contact with anaerobic bottom sediments.

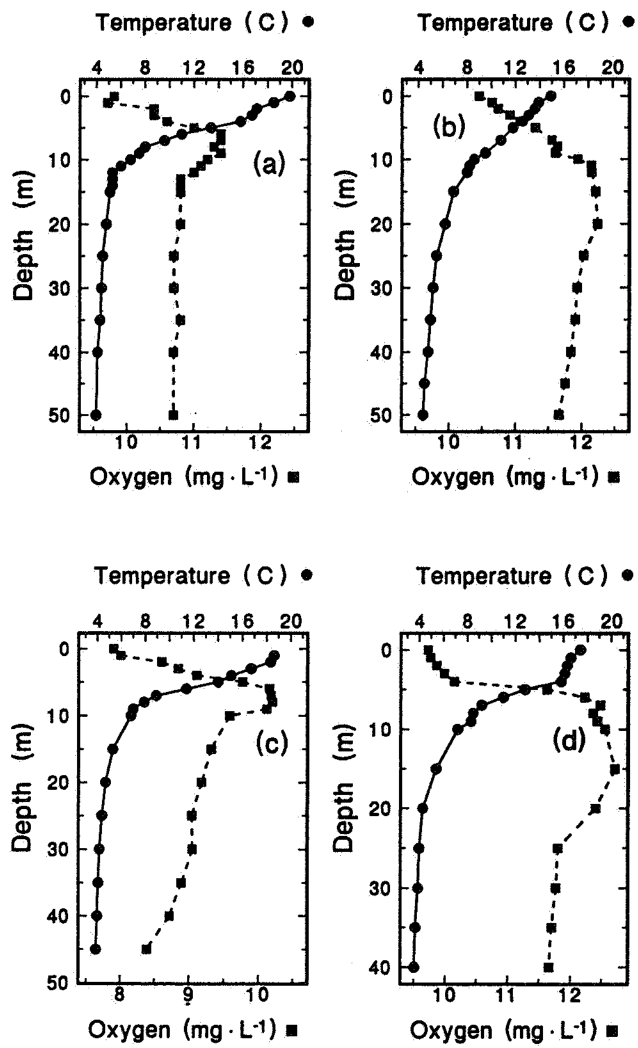

Figure 3.–Temperature and oxygen data collected from Walker Lake on 20 July 1993 (a), from Walker Lake on 7 July 1995 (b), from Takahula Lake on 18 July 1993 (c), from Takahula Lake on 7 July 1995 (d).

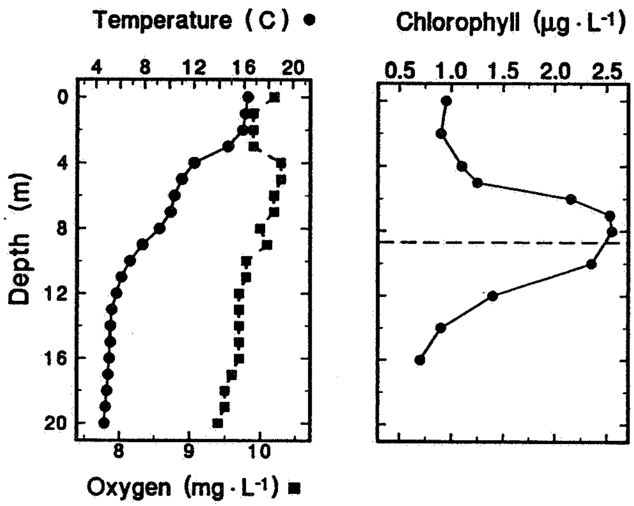

Figure 4.–Temperature and oxygen data collected from Narvak Lake on 13 July 1993 (left panel) and chlorophyll data within the water column (right panel), dashed line represents Secchi depth.

Water Clarity

Based on Alaskan lake criteria for turbidity (<2 NTU) and color (<16 Pt units) proposed by Koenings and Edmundson (1991) nine of the sampled lakes, located at elevations <740 m, were clear (Table 4). Among these, Secchi depth (SD) varied from 6.4 m (Nutuvukti) to 14.6 m (Takahula). In most cases these lakes were stratified and SD was located within a sub-surface algal peak (Fig. 4, Jones et al.1990) at temperatures averaging ~8.5°C cooler than the surface. In quadratic models, Chl and turbidity accounted for 88% and 75%, respectively, of the variation in 1/SD in these nine lakes. The strong correlation between Chl and NTU among these clear lakes ($r = 0.935$, $n = 9$) suggests that turbidity was largely of biogenic origin. Apparent color in a quadratic model accounted for 64% of the variation in 1/SD, which may include some effects of turbidity because samples for measurement of color were not filtered. At 1 m, median PAR was 60% of incident light and median light at the SD was ~3% which is the which is double and half, respectively, relative to PAR values in the water column of clear Alaskan lakes studied by Koenings and Edmundson (1991). The ratio of $I_{1\%}$ to SD in clear GAAR lakes was 1.5, which is about half the generally recognized value (Kirk 1994) and considerably less than the value of 2.4 in other clear Alaskan lakes (Koenings and Edmundson 1991). These differences were likely associated with increased light attenuation within the sub-surface algal peak and its influence on SD. Measured SD in these clear lakes

Table 4.–Light conditions (means) in lakes of Gates of the Arctic National Park and Preserve (lakes are in order of increasing altitude). [K_d(PAR) is the extinction coefficient of photosynthetically active radiation].

	K_d(PAR) (m^{-1})	Secchi Depth (m)	1% Light Depth (m)	Apparent Color (Pt-Co Units)	Turbidity (NTU)	Phytoplankton as Chlorophyll (µg·L-1)
Minakokosa[c]	–	5.8	–	14	–	1.7
Narvak[a]	0.433	8.7	10.4	12	0.36	1.5
Selby[c]	0.404	8.6	11.4	17	0.35	1.3
Nutuvukti[a]	0.433	6.4	10.4	16	0.43	1.6
Walker[b]	0.252	14.1	18.7	4.3	0.27	0.9
Takahula[b]	0.255	14.6	18.2	5.0	0.32	1.1
Matcharak[b]	0.330	7.8	14.0	9.4	0.56	2.3
Pingo[c]	–	–	–	20	–	2.1
Tulilik[c]	0.420	7.3	11.0	8.0	0.44	1.4
Itkillik[a]	0.290	9.2	16.0	12	0.42	1.1
Kipmik[b]	0.420	7.0	11.1	12	0.52	2.2
Chandler[b]	0.520	3.6	9.8	25	3.2	1.3
Kurupa[c]	1.53	0.6	3.0	83	18	0.5
Agiak[a]	0.464	4.8	10.3	25	1.1	1.7
Amiloyak[a]	0.262	4.6	17.6	19	1.1	1.6
Summit[a]	0.962	3.8	7.5	56	7.5	1.8

[a] Two years.
[b] Three years.
[c] One year.
[d] Dash means data were not collected.

are some 70% greater than empirical predictions (Jones and Bachmann 1978, Nürnberg 1996) because of non-uniform distribution of Chl within the water column. Our depth-integrated Chl measurements over-represented Chl values in the epilimnion, and therefore potential light scattering above the sub-surface algal peaks (Fig. 4). Among these clear lakes, K_d (attenuation coefficient) was significantly correlated with measures of stain – apparent color and $iron_{(log)}$ ($r = 0.7$ and 0.9, respectively) – but not with Chl or turbidity.

Among the study lakes, apparent color and turbidity increased with altitude, and both showed a strong cubic relation to the proportion of low biomass land cover types (prostrate shrub and barren land) in the catchment ($R^2 = 0.88$ and 0.82, respectively, $n = 16$). Lakes Agiak, Amiloyak and Chandler (>960 m) had moderate stain and SD averaged between 3.6 and 4.8 m (Table 3). Temperatures at the SD were <2°C cooler than the surface but there was no evidence of sub-surface algal peaks influencing light attenuation. SD in Agiak and Amiloyak matched empirical predictions using Chl (Jones and Bachmann 1978, Nürnberg 1996). These same equations over-predicted SD in Chandler Lake, perhaps because of its greater turbidity (Table 3); predicted SD improved when color was included with Chl (Nürnberg 1996). Among these three lakes the ratio of $I_{1\%}$ to SD averaged 2.9 which is about double the value in clear GAAR lakes but closely matches the recognized average (Kirk 1994).

Lake Kurupa was inundated with snowmelt and glacial rock flour at the time of sampling and measurements of apparent color and turbidity were near maximum, and SD (<1 m) was the minimum within this study. PAR at the SD was ~25 % of incident light and the ratio of $I_{1\%}$ to SD was 5, both of these metrics are consistent with light scattering by turbidity (Koenings and Edmundson 1991). Secchi transparency in Summit Lake varied in our two collections. Secchi was >6 m in 1993 when PAR at the SD was ~6% of incident light and the ratio of $I_{1\%}$ to SD was ~2, which is consistent with low turbidity and moderate stain. In 1995 we sampled as a massive debris flow caused by rainstorms entered the lake. SD was 1.1 m and measures of color and turbidity were some 5- and 15-times larger than in 1993 (LaPerriere 1999). These data indicate the potential for seasonal and annual fluctuations in factors regulating light attenuation in these remote lakes. Minakokosa and Pingo lakes were not included in the analysis because there were no light or turbidity data (Table 4).

Nutrients and Phytoplankton

Total phosphorus concentrations (TP) averaged between 3 and 15 $\mu g \cdot L^{-1}$ among GAAR lakes and total nitrogen (TN) averaged between 125 and 765 $\mu g \cdot L^{-1}$ (Table 3). The correlation between TP and TN was not significant but TP was significantly correlated with iron, color and turbidity ($r \geq 0.67$). Deep, low altitude lakes within the southern drainages had TP values of ≤ 5 $\mu g \cdot L^{-1}$ (Table 3). Values of TP >10 $\mu g \cdot L^{-1}$ were found in Kurupa and Summit lakes in 1995 when both lakes were influenced by turbid inflow. This was our only sample from Kurupa, but in 1993 TP in Summit was 6 $\mu g \cdot L^{-1}$, when turbidity was low; these measurements suggest summer inflows can sharply increase the TP content of some GAAR lakes. The highest TP and TN values were measured in Pingo Lake, the shallow oxbow with potential river influence (Table 3). Values of ≤ 175 $\mu g \cdot L^{-1}$ TN were measured only in high-elevation headwater lakes (Agiak, Amiloyak, Kipmik, Kurupa and Summit) and Chandler Lake in the high tundra (Table 2). Among the others, TN typically ranged between 200 and 360 $\mu g \cdot L^{-1}$, with > 400 $\mu g \cdot L^{-1}$ in Tulikik Lake, located in wet tundra with a high proportion of dense vegetation in the catchment (Table 2).

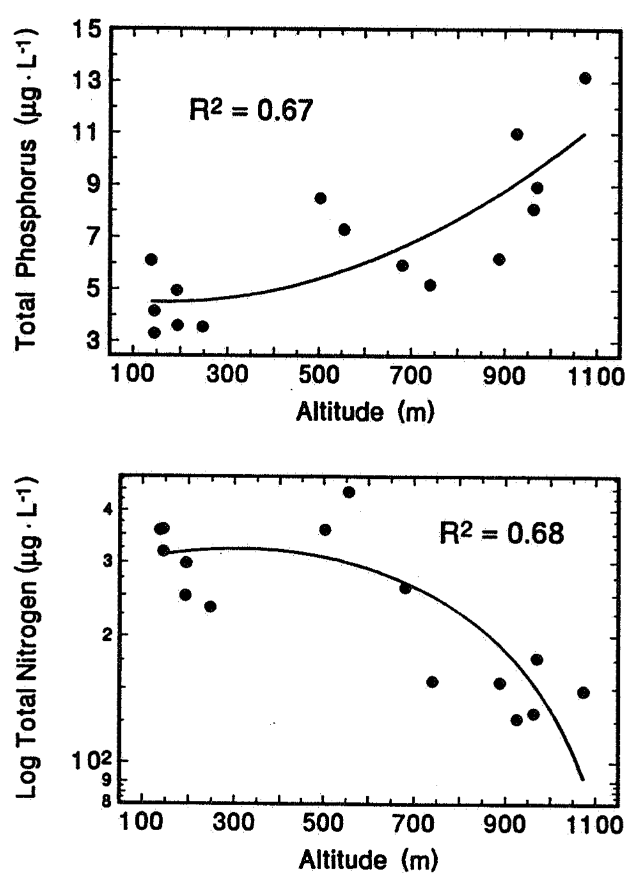

Figure 5.–Regression of total phosphorus and total nitrogen (log) on altitude for lakes within Gates of the Arctic National Park and Preserve.

Among these lakes, TP increased as a quadratic function of altitude ($R^2 = 0.67$, without Pingo, n =15, Fig. 5). Because of the effect of altitude on vegetation (Table 2), the TP relation was virtually identical when the proportion of sparse vegetation (prostrate shrub + barren land, $R^2 = 0.69$) in these basins was used as the independent variable, and TP decreased when the proportion of dense vegetation in the catchment (moist and wet tundra + tall shrub + spruce, $R^2 = 0.67$) was the independent variable. Uncertainty about mean TP levels in high altitude Kurupa and Summit lakes (Table 3) weakens our confidence in this analysis, but even without data from these lakes the relationship between TP and altitude was significant ($R^2 = 0.53$, n = 13) as were the relationships with sparse and dense vegetation ($R^2 = \sim 0.45$, p = 0.05).

In contrast to TP, the quadratic relationship between $TN_{(log)}$ and altitude was negative ($R^2 = 0.68$, n= 15, Fig. 5). Using vegetation as the independent variable, $TN_{(log)}$ decreased as a quadratic function of the proportion of sparse vegetation and increased with the proportion of dense vegetation. These landscape patterns were much weaker when the anomalously high-nutrient Pingo Lake was included in the analysis, presumably because of river influence or internal nutrient processes in this shallow, oxbow and thermocarst lake.

The TN:TP ratio showed a strong negative correlation with altitude (r = -0.94, n = 16, Fig. 6) and latitude (r = -0.84). Among the taiga lakes the TN:TP ratio was ~70, among tundra lakes at mid-altitude lakes it was ~40, and declined from ~20 to11 among high altitude lakes. Within the data set, TN:TP increased as a quadratic function of the proportion of dense vegetation in the catchment (moist and wet tundra + tall shrub + spruce) and decreased in a quadratic pattern with the proportion of sparse vegetation (prostrate shrub + barren land, $R^2 = \sim 0.7$). Nutrient concentrations in Pingo Lake were high relative to the other sampled GAAR lakes (Table 3) but at ~48 the TN:TP ratio was consistent with other GAAR lakes within the mid-altitude tundra. Likewise, the TN:TP ratio in Toolik Lake, located in tundra north of the Brooks Range at 720 m, has varied from 39 - 40 (Whalen and Cornwell 1985, Gregory-Eaves et al. 2000) to 55 (Kling et al. 2000). In eight small lakes within the Toolik basin this ratio was ~50 (Kling et al. 2000). In the Kuparuk River, a tundra stream in the region (Peterson et al. 1992), the ratio of dissolved forms of these nutrients averaged around 50.

Chlorophyll (Chl) averaged between 0.5 $\mu g \cdot L^{-1}$ in glacially fed Kurupa Lake to ~2 $\mu g \cdot L^{-1}$ in several study lakes (Table 3). Eliminating Kurupa Lake, where color and turbidity may have been important, the correlation between $Chl_{(log)}$ and $TP_{(log)}$ was 0.66 (n=15) and was virtually unchanged when lakes with TP >10 $\mu g \cdot L^{-1}$ were excluded. LaPerriere and Jones (2002) found Chl was responsive to TP in oligotrophic lakes elsewhere in Alaska, but most global Chl-TP models are weak when limited to lakes with TP <10 $\mu g \cdot L^{-1}$ (Watson et al. 1992, Nürnberg and Shaw 1998). The Chl:TP ratio averaged 0.25 among the GAAR lakes and ranged from 0.05 in Kurupa Lake, to ~0.4 in Selby and Kipmik lakes. This Chl:TP ratio closely matches the ratio for unproductive lakes in a global Chl-TP relation (Jones and Bachmann 1976) and lakes in the Yukon and NWT of Canada (Shortreed and Stockner 1986, Pientiz et al. 1997) but the GAAR value is about double the Chl:TP ratio of polymictic lakes on the Alaskan Katmai Peninsula (LaPerriere and Jones 2002). Subsurface algal peaks in many of the GAAR influence the overall Chl:TP ratio; paired samples show the Chl:TP ratio within the algal peak was double the surface value (0.2 versus 0.4, n=12). The ratio of Chl:TN (expressed as μg/mg) averaged 6.6, somewhat larger than other Alaskan lakes for which there are data (LaPerriere and Jones 2002). The correlation between Chl and TN was not significant but the data fit within the confidence limits of the Chl-TN relation of Canfield (1983).

Weight ratios of TN:TP suggest phosphorus limitation was likely among low altitude lakes and nitrogen limitation increased in importance in lakes at high altitude (Fig. 6). Nutrient Stimulation Bioassays confirmed this pattern (Table 3). Bioassays in Narvak, Selby, and Walker lakes (Jones et al. 1990, LaPerriere et al.1998) at altitudes <200 m, showed a significant response to phosphorus additions relative to the control and nitrogen. The TN:TP ratio was ~100 in these lakes during the experiments. In contrast, tests in lakes Agiak, Itkillik, Kipmik, Matcharak and Summit (altitude >500 m), responded to nitrogen additions over a range of TN:TP values of 7 in Summit Lake to ~40 in Itkillik Lake. In each of these experiments, there was a secondary response when both nutrients were added, indicating that our addition of the limiting nutrient outstripped the supply of the sufficient nutrient. The test in Chandler Lake was set when the lake was turbid from debris inflow and, relative to the initial Chl value, all treatments showed a response to light (Table 3) rather than nutrients.

Measurements of POC and PON in 1993 (Table 3) were highly correlated (r = 0.98, n = 12) and each showed a quadratic increase with altitude ($R^2 \geq 0.61$) such that, values among lakes at elevations <250 m (n = 5) were half the average measured in lakes located at >500 m (n = 7). POC and PON values were significantly correlated with TP values (r > 0.9, n =12), and negatively correlated with TN:TP ratios (r > -0.7) but neither measurement showed a significant relation with TN. Among GAAR lakes, PON averaged 11%

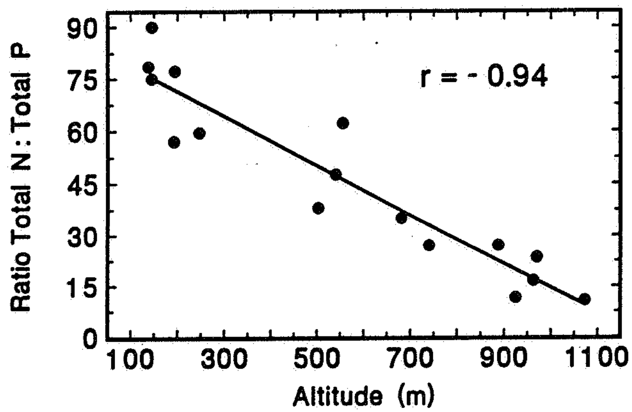

Figure 6.–Correlation of the ratio of total nitrogen-to-total phosphorus (TN:TP) with altitude for lakes within Gates of the Arctic National Park and Preserve.

(range 2 to 23%) of TN, and particulate P averaged 40% (range 25 to 59%) of TP, both proportions increased with altitude (r = > 0.83) and turbidity (r = >0.76). Values from Itkillik Lake (Table 3) closely match measurements from nearby Toolik Lake (Whalen and Conwell 1985). Using criteria for particulate matter by Hecky et al. (1993), molar ratios of C:N, C:P, N:P, and C:Chl suggest moderate nutrient deficiency of the phytoplankton was typical of GAAR lakes during 1993. The particulate composition ratio (as C:N:P molar ratio) of these lakes averaged ~200:20:1, which matches measurements from Toolik Lake (Kling et al. 2000) and other high latitude lakes (Hecky et al.1993).

Discussion

Consistent with other arctic lakes with undisturbed watersheds, GAAR lakes are oligotrophic based on concentrations of Chl <3.5 $\mu g \cdot L^{-1}$, TN <350 $\mu g \cdot L^{-1}$ and TP<10 $\mu g \cdot L^{-1}$ (Table 3, Nürnberg 1996). The exception, Pingo Lake a shallow oxbow and thermokarst lake sampled once, had mesotrophic nutrient levels (Fig. 1). Other lakes, also sampled once (Tulilik and Kurupa), had values of either N or P within the mesotrophic range (Table 2). In Summit Lake, TP was oligotrophic in 1993 and mesotrophic when the lake was inundated by a turbid debris flow in 1995 (LaPerriere 1999). Additional sampling of these lakes will show whether their trophic state differs from others within GAAR. Levels of TN (~290 $\mu g \cdot L^{-1}$), TP (~5 $\mu g \cdot L^{-1}$), and Chl (~1.4 $\mu g \cdot L^{-1}$) in much studied Toolik Lake (Kling et al. 2000), located northeast of the GAAR boundary, agree with our sample from that lake in July 1995, and closely match the median condition among our study lakes. Nutrient and Chl measurements from eight other lakes within the Toolik Lake watershed (Kling et al. 2000) also resemble values from the GAAR lakes. And Chl data collected by Levine and Whalen (2001) from 45 lakes near Toolik encompass the range found in GAAR (Table 3).

Most GAAR lakes are oligotrophic as judged by Secchi depth (>4 m, Nürnberg 1996). Among the clear GAAR study lakes (low turbidity and color, n =9) Chl was the primary light determining component with the SD often located within sub-surface algal peaks with Chl levels double the surface value, at ~3% of incident light (Fig. 4, Jones et al. 1990). In these lakes the ratio of $I_{1\%}$ to SD was1.5, thereby reducing the photic depth to a smaller fraction of water column relative to other clear lakes in Alaska (Koenings and Edmundson1991). Mineral turbidity, and less so color, controlled light in several high altitude lakes where turbid inflows were a factor. In these lakes, transparency is not a measure of lake trophic state.

The GAAR data show clear patterns between lake characteristics and landscape features. Local lithography explains the measured decrease in Ca equivalents and silica, and an increase in Mg with altitude because of calcareous rock in the southern basins and Mg-rich shale materials in the north. The decrease in lake temperatures with altitude and latitude observed during synoptic sampling is expected, and has been documented in other arctic lakes (Kling et al. 1992). Most interesting is the observed doubling of TP and concurrent halving of TN in GAAR lakes with altitude (Fig. 5). Both trends were correlated with the decreasing density of terrestrial vegetation, resulting in a sharp decline in the TN:TP ratio with altitude (Fig. 6, Table 3). An analysis of the relationships between TN and TP in world lakes by Downing and McCauley (1992) showed TN:TP declined rapidly with increasing TP in oligotrophic lakes. They attributed this pattern to natural, undisturbed watersheds exporting much less P than N. Our data match this finding (Fig. 6); GAAR lakes TN:TP significantly declined with increasing P (whether lakes Pingo, Summit and Kurupa, with the highest TP levels were included, or not). This pattern suggests that sources of these two nutrients change across the landscape continuum within GAAR described by altitude and vegetation zones (Table 2). In the arctic the composition and flux of elements from catchments is strongly influenced by watershed characteristics, such as vegetation (Kling 1995, Pienitz et al.1997, Levine and Whalen 2001).

Decreasing nitrogen content of GAAR lakes with increasing elevation (Table 3, Fig. 5) likely reflects decreasing N-fixation associated with the density of terrestrial vegetation in their catchments. Barsdate and Alexander (1975) found that biological N fixation accounts for most of the annual input of N to the arctic tundra, and even small scale variation in vegetation density can directly influence rates of N-fixation (Schell and Alexander 1973). We observed several non-leguminous N fixers (*Alnus, Myrica, Shepherdia,* and *Dryas,* Newcomb and Wood 1987) in the taiga and tundra, and a variety of lichens in these zones have associated free living or symbiotic cyanobacteria that fix N (Sprent and Sprent 1990, Thompson 1984). Leguminous N-fixers (family Fabaceae) are common in the floodplains in the taiga and tundra zones and on dry tundra sites. High nitrogen levels in streams draining to several of the taiga lakes (Jones et al. 1990, LaPerriere et al. 1998) and measurements of 1 $mg \cdot L^{-1}$ nitrate in the soil solution of the organic layer in the Walker Lake watershed (Ugolini et al. 1987) also support the conclusion of greater N-fixation in these watersheds than in the more sterile, high-altitude watersheds. Internal flux of nitrogen from the sediments has been shown in Toolik Lake (Whalen and Alexander 1986) but there are no estimates of whether this process occurs in the GAAR study lakes.

In headwater lakes (Agiak, Amiloyak, Kipmik, Kurupa and Summit) and Chandler Lake in the high tundra, where barren land and prostrate shrub dominate the catchments (Table 2), TN was ≤175 $\mu g \cdot L^{-1}$ (Table 3), which approximates the N content of regional rainfall (~190 $\mu g \cdot L^{-1}$, Kling et al.1992). Apparently, these high elevation catchments do not support abundant N-fixers in the terrestrial vegetation. The relation between TN and catchment vegetation among GAAR lakes is consistent with the landscape pattern measured in Canadian lakes in which concentrations of N species were higher in forest-tundra lakes than arctic and alpine tundra lakes (Pieniz et al. 1997) but opposite of the pattern in Central Europe where industrially enhanced atmospheric N deposition influences high altitude lakes (Kopáček et al. 1995, Kopáček et al. 1996).

The increase in TP in GAAR lakes with altitude (Fig. 5) is consistent with nutrient loading theory and in-lake processes determined by lake morphometry and stratification. Low P levels in low altitude lakes would be expected based on efficient retention of phosphorus by soils and vegetation (Whalen and Cornwell 1985, Peterson et al. 1992), and the potential for cold inflows to plunge deep in the water column of these stratified lakes (LaPerriere et al. 1998) thereby not having direct influence on our measurements of photic zone TP. In contrast, inflows from the barren rock and sparse vegetation prevalent in high altitude catchments directly influence the TP content shallow, polymictic lakes in the Brooks Range (Table 2). During spring runoff (Whalen and Cornwell 1985) and summer storms mountain lakes would be enriched with phosphorus, as demonstrated by our measurements of Kurupa and Summit lakes during turbid inflow in 1995. Significant correlations between TP and iron, apparent color and turbidity ($r \geq 0.67$) among GAAR lakes suggests particulate phosphorus is increasingly important in lakes at high elevation. Limited data from 1993 shows this was the case, particulate P increased with altitude ($r = 0.83$, $n = 12$) and composed ~30% of TP in low elevation lakes and >50% of TP in mountain lakes. The increase in particulate P in mountain lakes consistent with studies conducted in arctic lakes showing adsorption of P on iron hydroxides (Prentki et al. 1980), and an increase in particulate P in lakes where shale is present (Hamilton et al. 2001), such as the high elevation lakes in GAAR. High elevation lakes in GAAR likely have a greater supply of P than those at low elevation, and their shallow depth and polymictic thermal status favors mixing of external inputs within the water column. These findings are opposite of the pattern in the Tatra lakes (Central Europe) where TP levels were lowest in lakes surrounded by the least vegetation because of a lack of source in their catchment areas (Kopáček et al. 2000).

Across the landscape continuum within GAAR sources of these two nutrients change with increasing elevation. Declining supply of N to lakes with concurrent increases in P with altitude result in sharp decrease in TN:TP with elevation (Fig. 6). Among taiga lakes at low elevation this ratio was ~70, among tundra lakes at mid-altitude lakes it was ~40, and declined from ~20 to 11 among high altitude lakes. Within the data set, TN:TP increased as a quadratic function of the proportion of dense vegetation (moist and wet tundra + tall shrub + spruce) and the pattern was opposite with the proportion of sparse vegetation (prostrate shrub + barren land, $R^2 = \sim 0.7$ for both relations).

Ratios of TN:TP and Nutrient Stimulation Bioassays (Table 3) suggest phosphorus limitation was likely among low altitude lakes and nitrogen limitation increased in importance in lakes at high altitude. With TN:TP >25, several mid-altitude tundra lakes (Matcharak, Itkillik and Kipmik) would have been expected to respond to P rather than N. Our experimental response suggests not all of the TN was biologically available and phytoplankton were stimulated by additions of inorganic N. Studies in Toolik Lake, have shown a primary response to nitrogen additions, and that dissolved organic nitrogen is used to satisfy the N requirements of phytoplankton annually (Miller et al. 1986, Whalen and Alexander 1986). Toolik Lake has a TN:TP that varies between 39 and 55 (Whalen and Cornwell 1985, Kling et al. 2000) which is similar to the ratio measured in tundra lakes in our study. Enrichment bioassays conducted in lakes in the general vicinity of Tookik Lake (Levine and Whalen 2001), showed that N was generally more important than P in regulating phytoplankton.

This study documents basic lake characteristics within GAAR and shows how nutrients and nutrient limitation of phytoplankton differ along a landscape pattern of vegetation zones which are determined by altitude. Characteristics of tundra lakes within GAAR closely match much studied Toolik Lake and other lakes within its catchment (O'Brien et al.1997, Kling et al. 2000). Mountain lakes and lakes in remote, undisturbed locations, such as those in GAAR, should be monitored over time to assess how biogeochemical processes might change with circumpolar atmospheric pollutant transport, and climate change. In the case of GAAR lakes, potential oil and gas development on the northern park boundary may be an additional factor.

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